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Utilization of unadapted germplasm in soybean breeding populations

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ABSTRACT

Soybean [Glycine max (L.) Merr.] populations with 100%, 75%, 50%, 25%, and 0% unadapted germplasm were formed to study the effect of incorporating unadapted germplasm into a breeding population. Four selected adapted lines and four selected plant introductions were used as parents. Each population was intermated four to five times. Ninety-six randomly selected lines from each population were evaluated in three environments. Twenty-four of these lines from each population also were grown in a fourth environment.

The population means showed a small, but statistically significant decrease in yield with increasing percentages of unadapted germplasm. The population by environment interaction for yield was highly significant. Although most of the superior lines were identified from the populations with 0% and 25% unadapted germplasm, the highest yielding line was from the population with 75% unadapted germplasm. This would indicate that superior progeny can be selected from a population with a large percentage of unadapted germplasm, but the frequency of such lines is low. Genetic variance for yield was greatest in the populations that had both adapted and unadapted germplasm.

Height increased with increasing adapted germplasm reflecting the greater mean height of the adapted parents. Lodging scores increased with increasing percentage of unadapted germplasm.

INTRODUCTION

The germplasm base of cultivated soybeans in the United States is extremely narrow. In 1972, the six cultivars that were grown on a total of 56% of the production acreage traced to only 11 plant introductions. These same 11 plant introductions contributed to the ancestry of most of the remaining commercial cultivars (Johnson and Bernard, 1963; NAS, 1972). There has been no appreciable change in the situation since that date (Duvick, 1977).

The term "unadapted germplasm" has been used to refer to material which was developed in other habitats and includes native varieties and wild or weedy types. It encompasses those plants included in the primary gene pool of the crop, according to the proposed systematics of Harlan and deWet (1971).

The primary use of unadapted germplasm in soybean breeding has been as donor parents for genes for pathogen resistance in backcross programs, hence, new germplasm has been incorporated only in limited amounts. New cultivars have been largely the result of reselection within existing gene pools, further restricting the genetic variability. Not only is the crop potentially vulnerable to pathogens, but genetic advance for yield improvement may become limited (Allard and Hansche, 1964; Hanson, 1959a; Jensen, 1970; Kranz, 1973; NAS, 1972; Smith, 1971). Unadapted varieties of the crop can provide additional genetic variability for improvement of both qualitative and quantitative traits (Creech and Reitz, 1971).

The objective of this study was to determine the effect of the introgression of unadapted germplasm into adapted populations.

LITERATURE REVIEW

Unadapted germplasm has been used primarily as a source of genes for pest resistance in most crops (Harlan, 1976). It has had limited use as a source of additional genetic variability for quantitative trait improvement (Eberhart, 1970; Frey, 1976; Harlan, 1956; Hallauer and Malithano, 1976; Leffel and Hanson, 1961; Stephens et al., 1967). Exploitation of this variability has been restricted because breeders have been wary of incorporating genes into breeding populations that would result in unacceptable departures from agronomic standards. It also may result in the break-up of superior adapted gene complexes that were the result of plant breeding efforts (Griffing and Lindstrom, 1954; Krull and Borlaug, 1970; MacKey, 1954; Reeves, 1950; Rick, 1974; Simmonds, 1962).

Evaluation of Source Material

Selection and evaluation of parental varieties can be of significant value in improving a population (Eberhart, 1970; Eberhart, et al., 1967; Hallauer and Malithano, 1976). Marani (1963, 1964, 1967) reported good association between parental performances and general combining ability in interspecific crosses of cotton. The author concluded that selection of the parental varieties based on their yields would provide an indication of their progeny's performance.

Kramer and Ullstrup (1959) evaluated the combining ability of unadapted maize germplasm with a well-established single-cross hybrid.

They noted that although some of the plant introductions did provide additional genetic variability which resulted in higher yields, the greatest yield improvement was in crosses with unadapted lines which in themselves showed high yield potential.

Reeves (1950) used teosinte to improve the heat and drought tolerance of corn and found that improvement in these traits and accompanying increases in yield depended on the variety of teosinte used and on the adapted inbred selected. Need for selection of the adapted parent was explained by the presence of teosinte germplasm in many corn inbreds which limited the genetic divergence between some of the parents in the adapted by unadapted crosses and reduced heterosis (Reeves, 1950; Griffing and Lindstrom, 1954).

Thorne and Fehr (1970a) reported that population performance was generally predictable from parental performance in strains from 2-way crosses of adapted by unadapted parents. When a third, adapted parent was used in 3-way crosses, the differences among populations were smaller and less predictable.

A few studies have indicated that parental evaluation would be of little value. Niehaus and Pickett (1956) found essentially no correlation between F_1 progeny performance and unadapted parental yields in sorghum. Lawrence and Frey (1975) and Frey and Browning (1971) backcrossed Avena sterilis L., wild oats, into cultivated A. sativa L. lines and the yield increases were not predictable from the yields of the unadapted parents. They noted that the genetic background of the adapted parent influenced yield response.

Yield Responses Associated with Incorporation of Unadapted Germplasm

Yield increases attributed to the incorporation of unadapted germplasm have been reported in both autogamous and allogamous crops. The observed heterosis in wide crosses of cross-fertilized crops has been explained by the genetic diversity of the parental line. Wellhausen (1966) evaluated 300 intra- and inter-racial crosses using lines from the 25 races of maize in Mexico, as part of an effort to identify and utilize exotic maize germplasm complexes in indigenous varieties. The greatest heterosis was noted in crosses between the most diverse native races.

Wellhausen (1966) also compared the yields of two synthetic, open pollinated populations. The Celaya-Exotic population contained 50% exotic germplasm and was formed by compositing the progenies from crosses between the race Celaya and two other native races. The Celaya population was a composite of varieties most typical of the race Celaya. The Celaya-Exotic population was higher yielding than the Celaya population after three cycles of mass selection. Yield improvement was attributed to the heterosis associated with the use of diverse germplasm and from the additional genetic variability present in the other maize races.

Griffing and Lindstrom (1954) compared the yield from crosses with varying percentages of non-Corn Belt maize germplasm. Three classes of inbreds were used: lines developed from Corn Belt inbreds; acclimatized inbreds developed from Brazilian material that

probably traced back to southern U.S. dents and some native corn types; and exotic lines resulting from selections from crosses between Corn Belt inbreds and Mexican varieties. The highest yields were from crosses involving at least one exotic parent, but the greatest heterosis was in exotic by exotic crosses.

Moll et al. (1962) obtained hybrids from six maize varieties, two from the southwestern U.S., two from the Corn Belt, and two from Puerto Rico. Heterosis increased with increasing genetic diversity and highest yields involved progeny which had one Puerto Rican variety as a parent. Moll et al. (1965) expanded the study to include two southern Mexican varieties to determine if the relationship between genetic divergence and heterosis would be maintained in crosses of extremely divergent populations. Crosses were made within and between all groups, and the F_1 and F_2 populations were yield tested along with the parental populations in the four regions of adaptation. Crosses involving the Mexican parents, representing a population which was the most diverse from the other three, were lower yielding and showed reduced heterosis.

Goodman (1965) evaluated the use of exotic germplasm in maize breeding by comparing the estimates of genetic variance for yield from an adapted and a 50% exotic population. Superior West Indian varieties were crossed with Corn Belt single crosses and inbreds, and the progeny composited to form the 50% exotic population. The same ten commercial inbreds used in forming the West Indian Composite were mated to form the adapted population. Both composites underwent

minimum selection during the six generations of isolated open-pollination. Mean yield of the West Indian Composite was nearly equal to that of the Corn Belt composite, even though the latter was considered to be an elite source of adapted germplasm. The estimates of genetic variance for yield were greater for the West Indian composite. Therefore, the unadapted germplasm only slightly depressed the yield, yet provided a greater opportunity for further progress by selection through an increase in genetic variability.

Reeves and Bockholt (1964) obtained a few fertile hybrids from a cross of a highly adapted maize inbred and diploid Tripsacum dactyloides L. Progeny were backcrossed four to six times to the maize parent and then selfed. The derived lines contained 0.8-3.0% Tripsacum germplasm. Irregular chromosome behavior was observed and fertility was low prior to selfing. The derived lines were compared with the inbred parent in a space-planted nursery and in top-cross tests. Several lines had yields superior to that of the inbred and improved combining ability. Two defects of the inbred, top firing and chlorophyll breakdown, were either eliminated or reduced in expression in the improved lines.

Teosinte was incorporated into two commercial inbreds to improve their heat and drought tolerance (Reeves, 1950). A significant increase in the general combining ability in some BC_2 lines of one inbred was attributed to the introgression of teosinte germplasm. Mangelsdorf (1952) found an increase in yield in two strains which were the result of out-crossing a Texas inbred to teosinte, but there

was no improvement in general combining ability. The introgression of Tripsacum and teosinte has probably been important in the improvement of corn since its cultivation (Mangelsdorf, et al., 1964; Mangelsdorf and Reeves, 1959).

Malm (1968) used sorghum lines derived from African cultivars that were high yielding, early maturing, and tall to introduce additional genetic variability into U.S. cultivars. He determined that additional genetic variability for yield was present in African varieties when using four standard testers to determine the combining ability and yield potential of the modified exotic lines. He concluded that exotic sorghum varieties could be used to increase yields in the U.S. Niehaus and Pickett (1956) also noted striking heterosis in a diallel cross of three plant introductions and five U.S. sorghum inbreds when at least one parent was an unadapted inbred.

Interspecific crosses of Gossypium hirsutum L. and G. barbadense L. showed greater heterosis for lint yield than intraspecific crosses (Stroman, 1961). Heterosis of 6 to 38% for yield of seed cotton and lint in intraspecific crosses of G. hirsutum was associated with increased boll weight. Heterosis of 12 to 41% for yield in intraspecific crosses of G. barbadense was associated with number of bolls produced, but not an increase in boll weight. Increase in number of bolls was associated with a heterosis of 64 to 93% for yield in interspecific crosses in spite of lower boll weight (Marani, 1963, 1967).

The experience of the Swedish Seed Association in breeding autogamous plants has been that most two-way crosses between an adapted and an unadapted variety produce lines which are inferior to the adapted parent (MacKey, 1963). There have been a few exceptions, however, generally when the introduced line was similar in adaptation to the Swedish variety. An East German oat cultivar that was drought and frit fly resistant was successfully introduced into Sweden and was a parent of four released varieties (MacKey, 1963).

Winter wheat has been used by Pinthus (1967) and Grant and McKenzie (1970) to increase the yield and genetic diversity of spring wheat. Significant heterosis was noted in the yields of F_1 and F_2 populations from 2-way crosses when grown in a spring wheat environment. The greater number of spikelets per spike of the winter wheat was noted in the F_2 populations (Pinthus, 1967).

Fedak and Fejer (1975) obtained crosses between five winter barleys of interspecific origin and five spring barleys. Most of the F_1 populations exceeded the spring parent yield, although significant increases were noted only in space planted trials. The authors attributed the increased yields to the genetic diversity of the parents.

Backcrossing has been used extensively to incorporate unadapted germplasm into adapted cultivars in self-fertilized crops. Briggs (1935) and Briggs and Allard (1953) recommended at least six backcrosses to maximize recovery of the selected phenotype and minimize

the genetic contribution from the unadapted parent. Theoretically only 0.8% of the genome of a BC_6F_1 progeny would be from the unadapted parent, hence the technique would be most effective with qualitative traits which are simply inherited.

Sammeta and Rao (1966) compared the progenies from matings involving one, two and three backcrosses in wheat and suggested the use of only three backcrosses. They concluded that the additive contribution from the donor parent in a limited backcross scheme may result in better progeny, although the selected parental phenotype would not be recovered completely.

Unadapted Avena sterilis L. and A. sativa L. have been used as donor parents for resistance to Puccinia coronata Cda. avenae Frazier and Led. in the development of oat multiline cultivars. Frey and Browning (1971) reported that several isolines from BC_5 progenies had significantly higher yields than the recurrent parent when tested in disease-free environment. They attributed the increase to "linkage drag", the incorporation of "plus yield genes" closely linked to the qualitative genes being transferred.

Leininger and Frey (1962) studied the backcross variability of oats utilizing an A. sterilis line as the nonrecurrent parent. The grain yield of the progeny from the four backcross generations showed heterosis and a slower rate of regression toward the recurrent parent yield than would have been expected based on additive gene action alone. They suggested the possible use of backcrossing in quantitative trait improvement.

Jondle (1974) backcrossed genes for resistance to P. coronata from eight unadapted oat lines into three different genetic backgrounds. Homozygous resistant and susceptible F_2-, BC_1F_2-, and BC_2F_2-derived lines were evaluated for yield deviations associated with incorporation of genes for resistance. Yield genes associated with specific crown rust loci were transferred resulting in significant increase in grain yield in some progeny.

Lawrence and Frey (1975) studied the introgression of exotic oat germplasm from A. sterilis into adapted cultivars. Four wild oat lines were each backcrossed into two adapted lines and the progenies from each of the five backcross generations evaluated together with the parents. Although all of the A. sterilis parents were lower yielding than the adapted parents, they contributed genes which resulted in higher progeny yields. Takeda and Frey (1977) determined that these genes influenced yield by their control of growth rate. It was estimated that the A. sativa lines contributed about two-thirds of the yield genes and one-third was contributed by the A. sterilis lines (Lawrence and Frey, 1976). Transgressive segregants were noted in the progenies from the crosses involving three of the four exotic parents.

Williams (1969) compared the yields of single, three-way and backcrosses in oats between adapted, semi-exotic and exotic lines. Populations with increasing percentages of adapted germplasm were higher yielding, but the highest yielding progeny were obtained from crosses with one exotic parent. Single crosses between adapted

and semi-exotics produced progeny which yielded as expected, and lines from three-way crosses were higher yielding than parental means. Specific parental interactions were indicated and parental performance showed correlation with progeny performance.

Soybeans are a relatively new crop in the United States and as recently as 1937, 98 of the 101 varieties that were grown were either plant introductions, selections from plant introductions, or lines which resulted from natural outcrossing (Morse and Cartter, 1937). Only a few of these unadapted varieties were very productive in this country, and those were used as the foundation for the U.S. breeding programs (Hartwig, 1973). Consequently, there has been very little research into the use of unadapted lines in breeding populations to increase yields.

Thorne and Fehr (1970a,b) evaluated two- and three-way crosses to determine the effectiveness of using high protein, unadapted lines as a source of additional genetic variability for yield, protein and oil in soybeans. Two adapted parents were each crossed with three plant introductions and the F_1's from the six two-way crosses were mated with a third adapted parent. Transgressive segregants for yield were noted in all populations but the majority of superior lines were from three-way crosses.

Recombination

The success of using unadapted germplasm depends upon obtaining desirable recombinations. Genetic diversity needs to be maintained

for a selected number of generations to obtain effective breakup of linkage blocks and recombination (Hanson, 1959b). Selfing intensifies linkages and soon forecloses any option of genetic recombination outside of the narrow family lines of descent (Jensen, 1970). Based on theoretical models, Hanson (1959a) recommended 4-5 generations of intermating to obtain the major reduction in length of linkage blocks.

Wellhausen (1966) from his work with exotic maize races of Mexico, suggested five random mating without selection. Hallauer and Sears (1972) intermated the progeny from single crosses between the exotic Eto composite and six inbreds for two years using planned crosses. A bulk of the progeny from the last intermating was advanced through three additional cycles of recombination and mass selection for early silk emergence. The resultant synthetic variety, BS2, has shown good potential as a breeding population in the Corn Belt.

Suneson (1956) compared the yields of several bulk barley populations. The Composite Cross II (CCII) was developed by mechanically blending F_1 progenies from a diallel cross of 28 cultivars of diverse adaptation. The other populations were the result of matings between adapted cultivars. All populations showed progressive improvement for yield in successive generations of selfing which the author attributed to natural selection and recombination from occasional outcrossing. Although CCII was lower yielding than the adapted parents, its yield approximated that of the check variety in the F_{11} through F_{20} generation and was not significantly different in later generations.

Problems Associated with Direct Use of Unadapted Germplasm

Direct use of unadapted lines in a breeding program has not always been possible. Maize breeders had to use subtropical nurseries to obtain hybrids between U.S. maize and exotic and semi-exotic varieties (Efron and Everett, 1969; Griffing and Lindstrom, 1954). Hallauer and Sears (1972) found the maize exotic variety 'Eto Composite' too late and too tall for direct use in the Corn Belt. After initial hybridization of Eto to six early inbreds in a winter nursery, followed by three cycles of mass selection for early silking, they were able to obtain a synthetic usable in a Corn Belt breeding program. Eberhart (1971) suggested the use of subtropical nurseries for backcrossing and recurrent selection to develop semi-exotics from exotic and adapted varieties. These semi-exotics could be used directly by the breeder.

Stephens et al. (1967) converted unadapted sorghum varieties which were late maturing and too tall for U.S. commercial production to early, combine-height breeding lines for use in the temperate regions. They utilized short-day photoperiods in Puerto Rico during the winter for crossing and backcrossing. Desired phenotypes were selected in Texas during the regular growing season under long-day conditions.

James (1972) and Moore and Heinz (1971) were able to induce flowering of some unadapted Saccharum sp. by artificially modifying the photoperiod in greenhouse and field experiments to coincide with flowering of selected cultivars.

Grant and McKenzie (1970) noted problems with obtaining hybrids between spring and winter wheats due to divergent dates of pollination of the two types. They suggested that the spring habit could be backcrossed into selected winter wheat lines.

MATERIALS AND METHODS

Plant Material

The five populations used in this study were developed from four adapted lines and four plant introductions. The adapted parents included two cultivars, 'Chippewa 64' and 'Calland', and two experimental lines, C1426 (a sister line of Calland) and L15 (Wayne[6] x Clark 63) (Fehr and Clark, 1973). The adapted parents were high yielding and resistant to Phytophthora megasperma Drechs. var. sojae Hildeb. (race 1). The plant introductions, PI 68600, PI 68704, PI 81029, and PI 91150, were selected for their high yield potential in tests conducted by deMooy (1962) and Peterson (1967). PI 68704 and PI 81029 had a semi-determinate growth habit.

The five populations were formed using the mating scheme illustrated in Figure 1. The percentage of unadapted germplasm in each population was: AP1, 100%; AP2, 75%; AP3, 50%; AP4, 25%; AP5, 0%. Initial crosses for populations AP2 to AP5 were made in the summer of 1968 at Ames, Iowa, and for AP1 in 1969. Each random mating utilized a minimum of 30 male and 30 female S_0 plants. AP1 was intermated four times and the other populations five times. A minimum of 225 seed was obtained from the final mating of each population.

The S_0 seed from the last intermating was planted in Puerto Rico in November, 1972, and the S_0 plants were threshed individually. The progeny from each S_0 plant was considered an S_0 family. The S_1

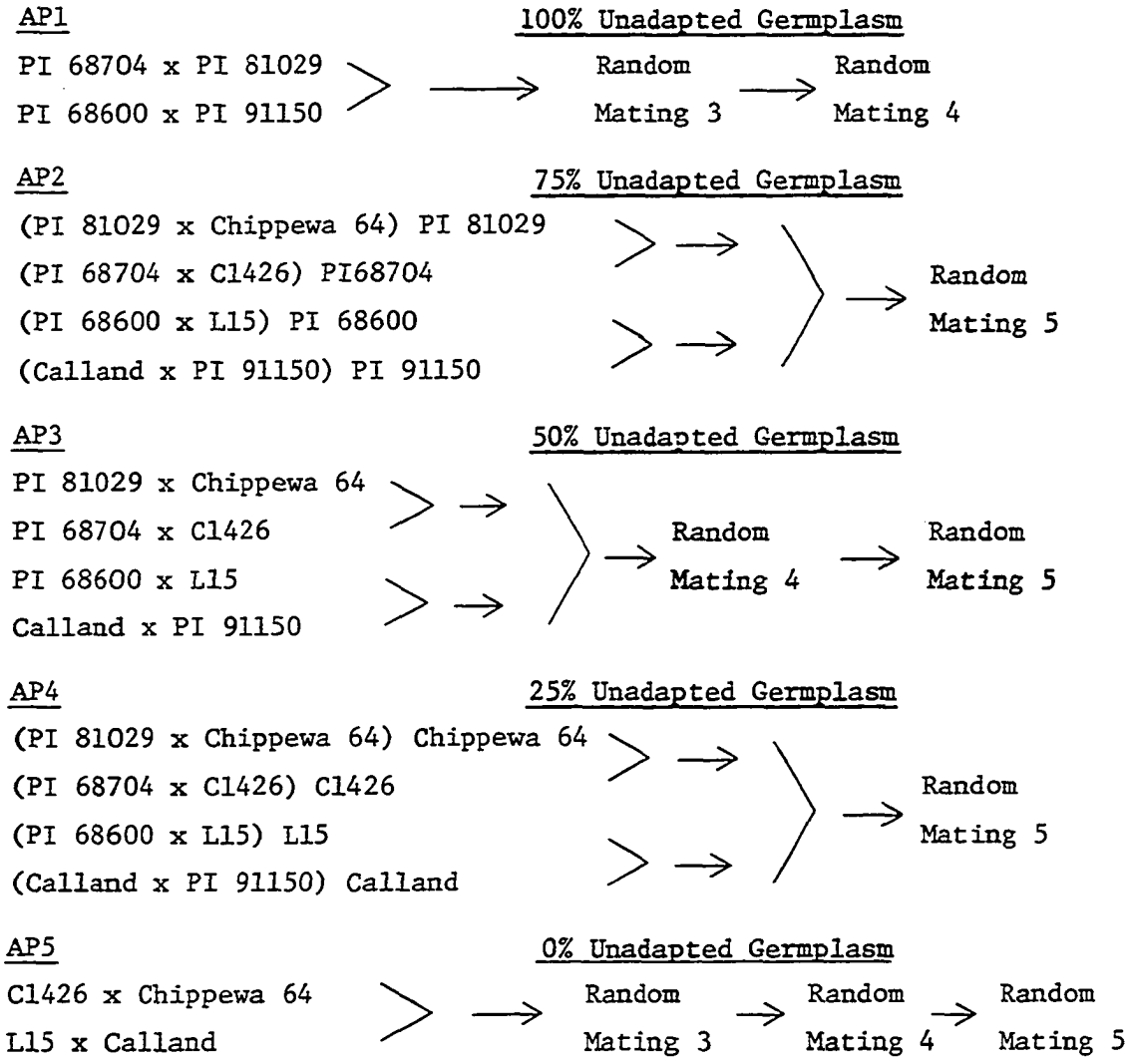


Figure 1. Mating scheme used in the formation of the five populations (Fehr and Clark, 1973)

seed from each S_0 plant was planted in a separate row in Puerto Rico in February, 1973, and one S_2 seed was harvested from each plant in a row. Each S_0 family was planted in a separate row at Ames in 1973, and two S_2 plants of 'Corsoy' maturity were harvested individually from each row. A random sample of eight S_3 seeds per S_2 plant were planted in a separate row in Puerto Rico during October, 1973, and one S_3 plant was randomly harvested from each row. The S_4 progeny was grown at Ames, 1974, and the row was harvested in bulk.

A pedigree was maintained during selfing to permit the use of as many different S_0 families as possible in the selection of S_3-derived lines for yield evaluation. From each of the five populations, 96 S_3-derived lines were selected representing 77 S_0 families. The primary basis for selection was time of maturity to assure a similar maturity for the lines from the five populations. The mean maturities and distributions of lines were similar and the maturity range was identical for the five populations (Table 1).

The 480 entries required a parcel of land of nearly one hectare per location for yield evaluation, therefore, blocking was used to reduce the effect of soil heterogeneity. Eight lines per population were included in a set of 40 entries. To minimize possible interplot competition due to maturity (Johnson and Bernard, 1963; Johnson, et al., 1955; Kwon and Torrie, 1964; Weber and Moorthy, 1952), entries were assigned to the sets on the basis of time of maturity. The maturity range within each of the 12 sets was 2 to 3 days based on nonreplicated maturity data from Ames, 1974. Sets were randomized within each replication as were entries within each set.

Table 1. Distribution for time of maturity of lines from the five populations for Ames 1974, 1975, and 1976

	Days relative to time of Corsoy maturity																
	$\bar{X}$	>4	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+6	+7	+8	+9	>9
Ames 1974[a,b]																	
AP1	+3.2				3	5	11	14	13	17	11	5	11	6			
AP2	+3.4				2	8	5	10	10	16	21	17	5	2			
AP3	+3.5				4	4	8	8	13	15	16	15	9	4			
AP4	+4.5				1	2	13	12	7	8	20	14	6	3			
AP5	+3.6				5	4	10	6	6	16	18	17	9	5			
Ames 1975[c]																	
AP1	+2.0	4	1	4	8	4	10	12	15	11	9	2	8	3	4		1
AP2	+2.3	1	1	2	3	5	10	22	17	15	7	6	1		2	2	2
AP3	+2.2	3	3	6	3	11	8	7	19	8	6	5	8		3	2	4
AP4	+2.8	2	5	2	1	5	8	17	14	9	12	3	3	4	4	2	4
AP5	+2.7	3	2	4	4	4	5	11	13	13	13	10	6	3	2	1	1
Ames 1976[c]																	
AP1	+3.0			2	1	2	6	17	12	12	10	12	11	3	6	1	
AP2	+3.4				2	4	4	10	11	13	13	19	6	8	4	1	1
AP3	+3.2			1	5	5	5	7	8	8	9	13	11	10	7	1	
AP4	+3.5			2	2	4	5	6	12	7	17	16	15	4	1	3	2
AP5	+3.2		1	1	5	3	5	10	11	8	9	11	11	11	3	4	

[a] AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[b] Scores based on one replication.

[c] Scores based on the mean of two replications.

The eight parents and three check cultivars, Corsoy, 'Wells', and 'Amsoy 71', were evaluated in a separate test grown adjacent to the main experiment. Parents and check cultivars were not included in each set to avoid interplot competition because the range of maturities for the parents was greater than that of the test lines. In addition, either less lines per population could have been tested or the size of the experiment would have had to be increased if the parents and checks had been included in each set. There were three replications of each parent and two of each of the check cultivars at each environment.

The 480 entries and the test of parents and checks were grown at Ames in 1975 and 1976, and at Stuart, Iowa in 1975. There were not adequate resources to test the entire set of lines at Stuart in 1976; therefore, only 24 lines per population and the parents and checks were evaluated. The earliest lines from each population were selected for testing at Stuart, 1976, to facilitate harvesting.

Test plots in each environment consisted of two rows 4.5 m long with 70 cm between rows within plots and 100 cm between plots. The center 3 m of both plot rows were harvested. Traits evaluated were:

Seed yield - kilograms per hectare, dried to a uniform moisture.

Time of maturity - days after 31 August when 95% of the pods had reached their mature pod color.

Lodging - scored at maturity, scale of 1.0 (all plants erect) to 5.0 (most plants prostrate).

Height - measured at maturity, centimeters from ground level to terminal bud.

The environment at Ames in 1975 was considered the most favorable. Plots at Ames in 1976 received moderate wind damage on 13 June, a severe hail storm on 26 June (70% leaf area destroyed) and a second hail storm on 29 June (nearly 100% of the leaf area destroyed and nearly 100% removal of the terminal buds on the main stems). For the remainder of the growing season, the plots received little additional precipitation.

Stuart was a lower yielding location due, in part, to drought both years. In 1975, the plot area was partially submerged for a short time due to an early season thunderstorm.

Experimental Design

The data were analyzed using the following model to test for the effect of sets:

$$Y_{ijkl} = \mu + R_i + S_j + P_k + (PS)_{jk} + L_{jkl} + e_{ijkl}$$

where

$R_i = i^{th}$ replication; i = 1 to 2

$S_j = j^{th}$ set; j = 1 to 2

$P_k = k^{th}$ population; k = 1 to 5

$(PS)_{jk}$ = interaction of the j^{th} set and the k^{th} population

L_{jkl} = l^{th} line in the k^{th} population in the j^{th} set; l = 1 to 8

e_{ijkl} = higher order interactions, replication interactions, and random error.

The effect of sets, which was a measure of the blocking on maturity, was generally nonsignificant (Table 2), therefore, it was deleted from the combined analysis of variance model. For the combined data, the model was:

$$Y_{ijkl} = \mu + E_i + R_{ij} + P_k + (EP)_{ik} + L_{kl} + (EL)_{ikl} + e_{ijkl}$$

where

E_i = i^{th} environment; i = 1 to 4

R_{ij} = j^{th} replication in the i^{th} environment; j = 1 to 2

P_k = k^{th} population; k = 1 to 5

$(EP)_{ik}$ = interaction of the i^{th} environment with the k^{th} population

L_{kl} = l^{th} line in the k^{th} population; l = 1 to 96

$(EL)_{ikl}$ = interaction of the i^{th} environment with the l^{th} line in the k^{th} population

e_{ijkl} = higher order interactions, replication interactions and random error.

Analysis of variance and expected mean squares are presented in Table 3.

Estimates of variability among lines and the environment x line interaction were obtained for each population. The mean squares for the environment x line interaction were not significantly different among populations for all traits using Bartlett's test for homogeneity of variances (Snedecor and Cochran, 1972). The sum of squares for the environ-

Table 2. Analysis of variance for yield at Ames and Stuart, 1975 and Ames, 1976, using the complete entry set of 96 lines per population

Source of variation	Degrees of freedom	Mean squares		
		Ames 1975	Stuart 1975	Ames 1976
Replication (R)	1	20287064.4**	379977.1	91.7
Set (S)	11	1704749.9	1617993.2	1658815.2*
Error A	11	1126955.9	361332.8	419398.1
Population (P)	4	789189.8**	2494775.6**	1245329.5**
Linear	1	1947109.6**	9461875.2**	142373.4
Quadratic	1	859327.8**	289344.6**	4514102.9**
Lack of fit	2	175161.0	113941.3	162421.0
S x P	44	153750.1**	38184.7	212516.8**
Error B	48	59269.4	28311.9	95306.9
Line/PS	420	114154.1**	69016.4**	245864.5**
Error C	420	6513.1	22969.6	78836.6[a]
Corrected total	959			

[a]Four missing plots, therefore degrees of freedom = 416.

*,**F values are significant at 5% and 1% probability levels, respectively.

Table 3. Analysis of variance and expected mean squares for the combined model

Source of variation	Degrees of freedom	Expected mean squares
Environment (E)	e-1	$\sigma^2_{R(E)P} + p\sigma^2_{R(E)} + rp\sigma^2_E$
Replication/E (R/E)	(r-1)e	$\sigma^2_{R(E)P} + p\sigma^2_{R(E)}$
Population (P)	p-1	$\sigma^2_{R(E)P} + r\frac{p}{p-1}\sigma^2_{EP} + ep\sum_k P_k/p-1$
E x P	(e-1)(p-1)	$\sigma^2_{R(E)P} + r\frac{p}{p-1}\sigma^2_{EP}$
Error A	(r-1)e(p-1)	$\sigma^2_{R(E)P}$
Lines/P (L/P)	$(\ell-1)p$	$\sigma^2_{R(E)L(P)} + r\sigma^2_{EL(P)} + re\sigma^2_{L(P)}$
E x L/P	$(e-1)(\ell-1)p$	$\sigma^2_{R(E)L(P)} + r\sigma^2_{EL(P)}$
Error B	$(r-1)e(\ell-1)p$	$\sigma^2_{R(E)L(P)}$

ment x line interaction were pooled across populations and the pooled mean square was used to estimate the genetic variance components from the following relationship:

$$\sigma_g^2 = \frac{MS_L - MS_{ExL(P)}}{re}$$

where

σ_g^2 = genotypic variance

$MS_{L(P)}$ = mean square for lines

MS_{ExL} = mean square for environment x line interaction

r = number of replications

e = number of environments.

The variances of the genetic variance components were estimated by the relationship (Anderson and Bancroft, 1952):

$$\sigma^2(\sigma_g^2) = \frac{2}{(er)^2}\left[\frac{MS_L^2}{\ell+1} + \frac{MS_{ExL(P)}^2}{(\ell-1)(r-1)+2}\right]$$

where

MS_L = mean square for lines

$MS_{ExL(P)}$ = mean square for environment x line interaction

e = number of environments

r = number of replications

ℓ = number of entries.

RESULTS

Direct comparisons of the populations with the parents cannot be made because they were grown in separate tests. Comparisons between the adapted and unadapted parents showed that the adapted parents on the average were higher yielding, later maturing, taller and lodged less than the unadapted parents (Table 4). The lower yield of the plant introductions was due primarily to their earlier maturity. Coefficients derived from the regression of yield on time of maturity were used to adjust parent yields. There was no significant difference between the adjusted yields of the eight parents (Table 5).

Yield

The differences between all populations were small, but as the percentage of adapted germplasm in a population increased, the mean yield of the population increased (Table 6). The exception was AP1 (100% unadapted germplasm) which was higher yielding than AP2 (75% unadapted germplasm). Although AP2 had the lowest mean yield, the highest yielding line in the test was from this population. In all environments, fewer than 5% of the lines within each population exceeded the mean yield by more than two standard deviations (Tables 7 and 8). Generally AP5 had the greatest number of lines which exceeded the mean by at least one standard deviation, and fewer that were one standard deviation or more below the mean.

Table 4. Mean yield, time of maturity, height, and lodging score for parents and check cultivars

	Yield (kg/ha)					Time of maturity[2]				
	Ames 1975	Stuart 1975	Ames 1976	Stuart 1976	Mean	Ames 1974	Ames 1975	Ames 1976	Stuart 1976	Mean[3]
Chippewa 64[1]	2038f	1458g	1863de	2056f	1854e	20	-1g	11h	4f	5e
C1426	2976b	2024c	2444c	2646c	2522b	32	16b	20c	10c	15b
L15	3501a	2270b	2777b	2937a	2871a	36	24a	25a	13a	21a
Calland	3564a	2201b	2986a	2634c	2846a	38	24a	23b	11b	20a
PI 68600	2469cd	1683f	2366c	2192e	2178cd	31	7f	16e	5e	9d
PI 81029	2454de	1842d	1860de	2643c	2200c	28	8e	12g	6d	9d
PI 91150	2373e	1788e	1786e	2445d	2098d	30	9d	15f	6d	10cd
PI 68704	2555c	1779e	1914d	2803b	2263c	31	10c	17d	6d	11c
Adapted parent mean	3020	1988	2518	2568	2523	32	16	20	10	15
Unadapted parent mean	2463	1773	1981	2521	2184	30	8	15	6	10
Corsoy	2828	1830	2148	2567	2343	26	10	13	4	9
Wells	2418	1772	2181	2670	2260	--[4]	10	18	6	11
Amsoy 71	2719	2049	2090	2627	2371	32	11	16	6	11

[1]Values followed by the same letter are not significantly different from each other at the 5% probability level according to Duncan's New Multiple Range Test.

[2]Days after 31 August.

[3]Based on Ames, 1975 and 1976, and Stuart, 1976.

[4]No data recorded.

Table 4. (continued)

	Height (cm)				Lodging score[5]			
	Ames 1975	Stuart 1975	Stuart 1976	Mean	Ames 1975	Stuart 1975	Stuart 1976	Mean
Chippewa 64	72g	70e	64g	69e	1.1d	1.0f	1.5e	1.2f
C1426	96c	81b	80c	86b	1.4cd	2.8c	1.5e	1.9e
L15	114a	83a	91a	96a	2.5b	4.0a	1.7c	2.7a
Calland	99b	78c	87b	88b	1.7c	2.3d	1.6d	1.9e
PI 68600	92d	72d	78c	81c	2.7ab	2.2d	1.9a	2.3bc
PI 81029	76f	64g	69f	70e	3.0a	2.0e	1.8b	2.2cd
PI 91150	72g	60h	72e	68e	1.7c	2.8c	1.5e	2.0de
PI 68704	79e	67f	75d	74d	2.7ab	3.0b	1.7c	2.5ab
Adapted parent mean	95	78	80	85	1.7	2.5	1.6	1.9
Unadapted parent mean	80	66	74	73	2.5	2.5	1.7	2.2
Corsoy	87	64	71	74	2.2	1.2	1.5	1.6
Wells	86	67	80	78	1.2	2.0	1.4	1.5
Amsoy 71	99	80	85	88	2.0	3.2	1.6	2.3

[5]Scale of 1 (all plants erect) to 5 (most plants prostrate).

Table 5. Mean yield for parents adjusted for time of maturity

	Ames 1975	Ames 1976	Stuart 1976	Mean
Chippewa 64[a,b]	2754	2297	2381	2477
C1426	2781	2286	2424	2497
L15	2754	2062	2678	2498
Calland	2733	2516	2384	2544
PI 68600	2825	2561	2387	2591
PI 81029	2761	2254	2761	2592
PI 91150	2591	2021	2491	2368
PI 68704	2737	2007	2849	2531
Adapted	2756	2290	2467	2504
Unadapted	2728	2211	2622	2520

[a]Kg/ha

[b]No significant difference between entries within columns according to Duncan's New Multiple Range Test.

Table 6. Mean yield and time of maturity for Ames and Stuart, 1975 and 1976, using the complete entry set of 96 lines per population and the partial entry set of 24 lines per population

	Complete entry set				Partial entry set				
	Ames 1975	Stuart 1975	Ames 1976	Mean	Ames 1975	Stuart 1975	Ames 1976	Stuart 1976	Mean
Yield (kg/ha)[1,2]									
AP1	2948b	1821d	2143b	2304b	2795bc	1739e	2017b	2403a	2239b
AP2	2887c	1824d	2022b	2244c	2789c	1805d	1856c	2283d	2183b
AP3	2926b	1929c	2024b	2293bc	2741d	1832c	1988b	2310c	2218b
AP4	3004a	1993b	2018b	2338b	2948a	1878b	1785d	2365b	2244b
AP5	3048a	2088a	2188a	2441a	2831b	1967a	2144a	2356b	2324a
Mean	2963	1931	2079	2324	2821	1844	1958	2343	2242
Time of maturity[3]									
AP1	11.5c	-[4]	16.0b	13.8c	9.8a	-	14.9a	5.1a	9.9a
AP2	11.8b	-	16.4a	14.1b	10.0a	-	14.7ab	4.9b	9.9a
AP3	11.7bc	-	16.2ab	14.0bc	8.8b	-	14.1b	4.7c	9.2b
AP4	12.3a	-	16.5a	14.4a	10.0a	-	14.6ab	4.9b	9.8a
AP5	12.2a	-	16.2ab	14.2ab	8.6b	-	13.1c	4.6d	8.7c
Mean	11.9	-	16.3	14.1	9.4	-	14.3	4.8	9.5

[1] AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[2] Values followed by the same letter are not significantly different from each other at the 5% probability level according to Duncan's New Multiple Range Test.

[3] Days after 31 August.

[4] No data recorded.

Table 7. Distribution of entries by mean yield in relation to each environment mean using the complete entry set of 96 lines per population

	Standard deviation								
	-5	-4	-3	-2	-1	0	1	2	3
Ames 1975[a]									
AP1				2	13	67	13	1	
AP2				1	21	67	5	1	1
AP3				2	14	67	13		
AP4				1	11	68	13	3	
AP5					4	68	23	1	
Stuart 1975									
AP1			1	7	27	56	5		
AP2		1	3	5	24	60	2		1
AP3			1	4	12	57	17	5	1
AP4				1	10	58	21	5	1
AP5				1	2	43	37	13	
Ames 1976									
AP1			1	2	8	68	17		
AP2	1	1		8	8	62	15	1	
AP3		1	4	4	14	54	15	4	
AP4			2	6	14	60	10	4	
AP5			3		8	56	23	5	1
$\bar{X}$									
AP1					10	81	5		
AP2			2		12	81		1	
AP3				1	14	74	7		
AP4				1	8	77	10		
AP5					5	69	21	1	

[a] AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

Table 8. Distribution of entries by mean yield in relation to each environment mean using the partial entry set of 24 lines per population

	Standard deviation								
	-4	-3	-2	-1	0	1	2	3	4
Ames 1975[a]									
AP1				3	18	3			
AP2				4	16	4			
AP3				6	15	3			
AP4				3	13	7	1		
AP5				2	21	1			
Stuart 1975									
AP1			3	8	12	1			
AP2			1	4	16	3			
AP3		1	1	2	14	5	1		
AP4			2	1	14	7			1
AP5				2	13	7	2		
Ames 1976									
AP1				2	16	6			
AP2	1		3	3	14	3			
AP3		2		3	13	5	1		
AP4		2	1	3	17	1			
AP5					16	7	1		

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

Table 8. (continued)

	-4	-3	-2	-1	0	1	2	3	4
Stuart 1976									
AP1			1		16	5	2		
AP2			2	7	10	5			
AP3				5	16	3			
AP4				4	17	2			1
AP5				5	15	4			
$\bar{X}$									
AP1					24				
AP2			1	2	21				
AP3				1	22	1			
AP4				3	19	2			
AP5					23	1			

There was a highly significant population x environment interaction (Tables 9 and 10). The graph of yield versus percentage unadapted germplasm illustrates the different responses to the environments (Figure 2). In general, the partial entry set of 24 lines per population at four environments showed similar trends to the complete entry set of 96 lines per population in the three environments.

The genetic variance component was greatest in AP3 and smallest in AP1 and AP5. However, there was no statistical difference between variances except at Ames, 1976 (Tables 11 and 12). The differences among populations were consistent with their parental composition. AP1 and AP5 had four parents each, and AP2 and AP4 had eight parents (half of the parents of AP2 and of AP4 contributed 75% of the genes) and AP3 had all parents represented equally.

Time of Maturity

Three of the four adapted parents matured later than the check varieties and the fourth, Chippewa 64, matured earlier. All the unadapted parents matured within the range of the check varieties. The mean time of maturity was later for the adapted parents than for the unadapted parents (Table 4). Although some of the population differences were statistically significant, the variation was not large enough to explain the differences among populations for yield.

Table 9. Analysis of variance for yield for the combined data for Ames and Stuart, 1975, and Ames, 1976, using the complete entry set of 96 lines per population

Source of variation	Degrees of freedom	Mean squares
Environment (E)	2	298765164.6
Replication/E (R/E)	3	45109781.9**
Population (P)	4	3132531.7*
Linear	1	7836723.9**
Quadratic	1	4294953.4**
Lack of fit	2	199224.3
E x P	8	698381.6**
Error A	12	63082.9
Line/P[a] (L/P)	475	248652.7**
AP1	95	177662.7**
AP2	95	274165.8**
AP3	95	303875.2**
AP4	95	275239.8**
AP5	95	212320.0**
E x L/P	950	128764.8**
AP1	190	107598.2**
AP2	190	143721.9**
AP3	190	147758.4**
AP4	190	119622.8**
AP5	190	125124.1**
Error B	1424[b]	69378.7
Corrected total	2875	

[a] AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[b] Ames 1976 data had four missing plots.

*,** F values are significant at 5% and 1% probability levels, respectively.

Table 10. Analysis of variance for yield for the combined data for Ames and Stuart, 1975 and 1976, using the partial entry set of 24 lines per population

Source of variation	Degrees of freedom	Mean squares
Environment (E)	3	46148548.1**
Replication/E (R/E)	4	1631515.0**
Population (P)	4	536567.3
Linear	1	1129823.6
Quadratic	1	927619.4
Lack of fit	2	44412.7
E x P	12	332243.5
Error A	16	36217.5
Line/P[a] (L/P)	115	207692.3**
AP1	23	96083.8
AP2	23	275318.0**
AP3	23	294487.9**
AP4	23	255607.0**
AP5	23	116964.7
E x L/P	345	109993.6**
AP1	69	97648.8**
AP2	69	138853.9**
AP3	69	132498.1**
AP4	69	109150.8**
AP5	69	71816.4**
Error B	460	58731.2
Corrected total	959	

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

**F values are significant at 1% probability level.

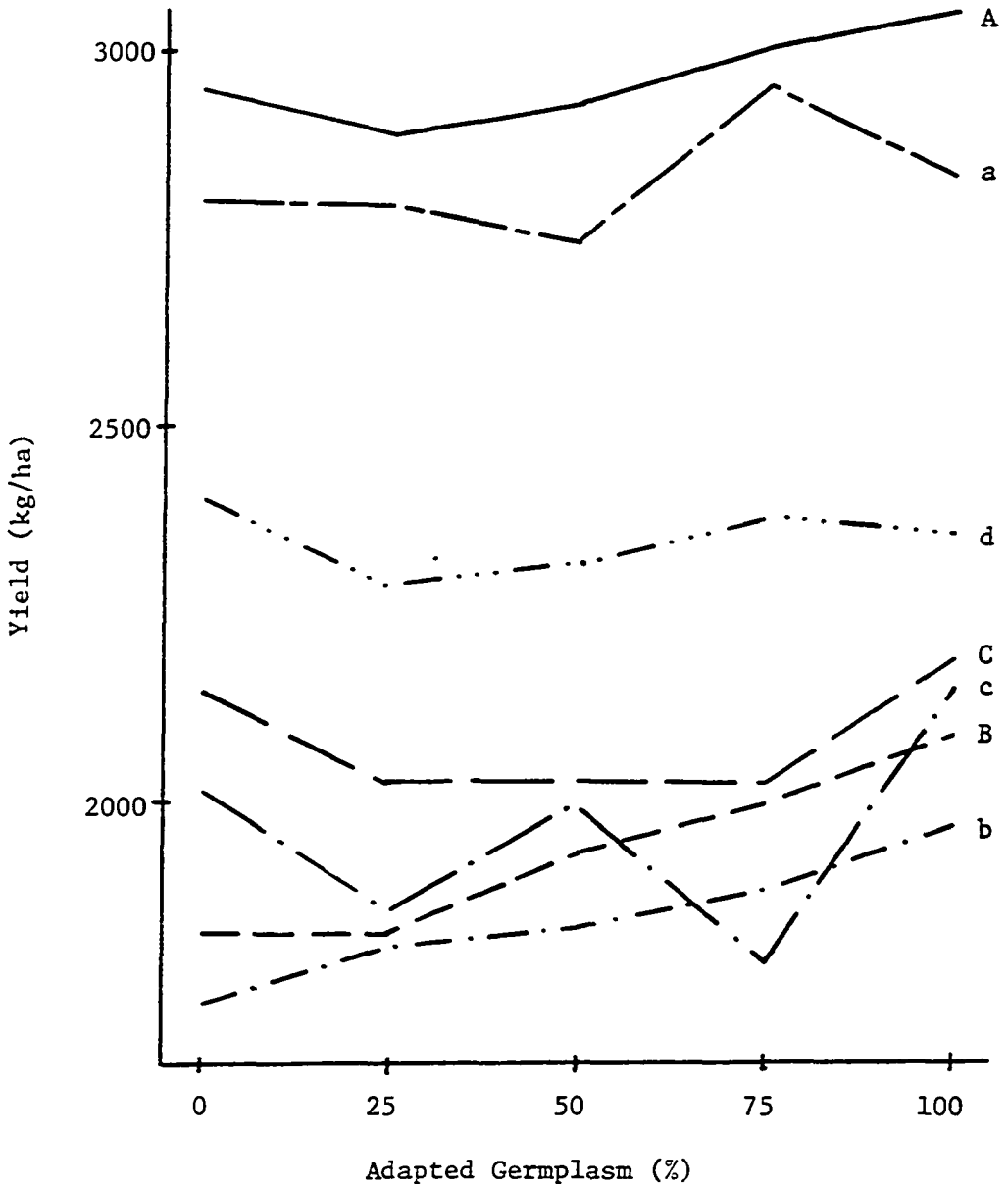


Figure 2. Mean yield of the five populations using the complete entry set of 96 lines per population at (A) Ames, 1975, (B) Stuart, 1975, (C) Ames, 1976, and the partial entry set of 24 lines per population at (a) Ames, 1975, (b) Stuart, 1975, (c) Ames, 1976, and (d) Stuart, 1976

Table 11. Estimated genetic variance and standard error for yield and time of maturity for Ames and Stuart, 1975, and Ames, 1976, using the complete entry set of 96 lines per population

	Ames 1975	Stuart 1975	Ames 1976	Combined
Yield (kg/ha)[a,b]				
AP1	31913 ± 12749a	16558 ± 5140a	43593 ± 14068b	8150 ± 4783a
AP2	38076 ± 13520a	27166 ± 6544a	111197 ± 23156a	24234 ± 6917a
AP3	39452 ± 13695a	29065 ± 6801a	126808 ± 25321a	29185 ± 7595a
AP4	29961 ± 12508a	25107 ± 6268a	97807 ± 21313ab	24413 ± 6942a
AP5	23421 ± 11712a	13968 ± 4808a	89530 ± 21081ab	13926 ± 5533a
Time of maturity[b,c]				
AP1	10.6 ± 1.7a	-[d]	5.3 ± 1.0a	5.9 ± 1.1a
AP2	7.6 ± 1.3a	-	4.7 ± 0.9a	4.7 ± 0.9a
AP3	12.7 ± 2.0a	-	7.7 ± 1.4a	8.5 ± 1.5a
AP4	13.8 ± 2.2a	-	5.9 ± 1.1a	8.1 ± 1.4a
AP5	10.9 ± 1.8a	-	7.6 ± 1.3a	7.8 ± 1.4a

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[b]Values followed by the same letter are not significantly different from each other since their ranges, as indicated by two standard errors on either side, overlap.

[c]Days after 31 August.

[d]No data recorded.

Table 12. Estimated genetic variance and standard error for yield and time of maturity for Ames and Stuart, 1975 and 1976, using the partial entry set of 24 lines per population

	Ames 1975	Stuart 1975	Ames 1976	Stuart 1976	Combined
Yield (kg/ha)[a,b]					
AP1	17607±21016	15492±9373	26746±25542	17204±8885	-1739[c]±4107
AP2	37397±25734	13352±8831	154964±59354	22763±10357	20666±10004
AP3	34760±25083	31693±13646	146114±56923	15963±8561	23062±10664
AP4	47198±28189	20835±10754	83347±39940	22690±10336	18202±9327
AP5	-820[c]±17106	14307±9072	25425±25229	9831±6961	871±4736
Time of maturity[b,d]					
AP1	4.9 ± 1.8	-[e]	3.3 ± 1.5	1.0 ± 0.4	1.7 ± 0.7
AP2	2.7 ± 1.2	-	3.5 ± 1.5	1.1 ± 0.4	1.3 ± 0.6
AP3	8.0 ± 2.7	-	7.0 ± 2.5	1.7 ± 0.6	4.2 ± 1.4
AP4	7.0 ± 2.4	-	5.1 ± 2.0	± 0.3	2.7 ± 1.0
AP5	8.0 ± 2.7	-	3.1 ± 1.4	± 0.3	2.5 ± 1.0

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[b]Values within each column are not significantly different from each other since their ranges, as indicated by two standard errors on either side, overlap.

[c]Estimated by zero.

[d]Days after 31 August.

[e]No data recorded.

Time of maturity was used as a criterion for selection of the lines within each population. Although there were slight shifts in the mean and the distribution for the time of maturity relative to Corsoy, the five populations responded similarly in each environment (Table 1 and Figure 3).

Height

With the exception of Chippewa 64, all the adapted parents were taller than the unadapted parents (Table 4). PI 68704 and PI 81029 had a semi-determinate growth habit. PI 91150 appeared to have an indeterminate growth habit but its height was similar to the two semi-determinate lines.

The average height of the populations tended to increase as the percentage of adapted germplasm increased (Table 13). The complete data set showed a highly significant linear response (Table 14). The effect of environments can be seen in Figure 4; however, the environment x population interaction was significant only in the analysis of the partial data set (Table 15).

The largest estimates of genetic variance for height were for AP4. The estimate for AP1 was statistically lower than for AP4 only in the complete entry set at Stuart, 1975, and in the combined combined analysis (Tables 16 and 17). The low estimate for AP1 may have been due to the semi-determinate growth habit, which may have diminished the expression of the other height genes that might have been present in the population. The greatest amount of genetic variability would be expected in AP2 to AP4 since those populations

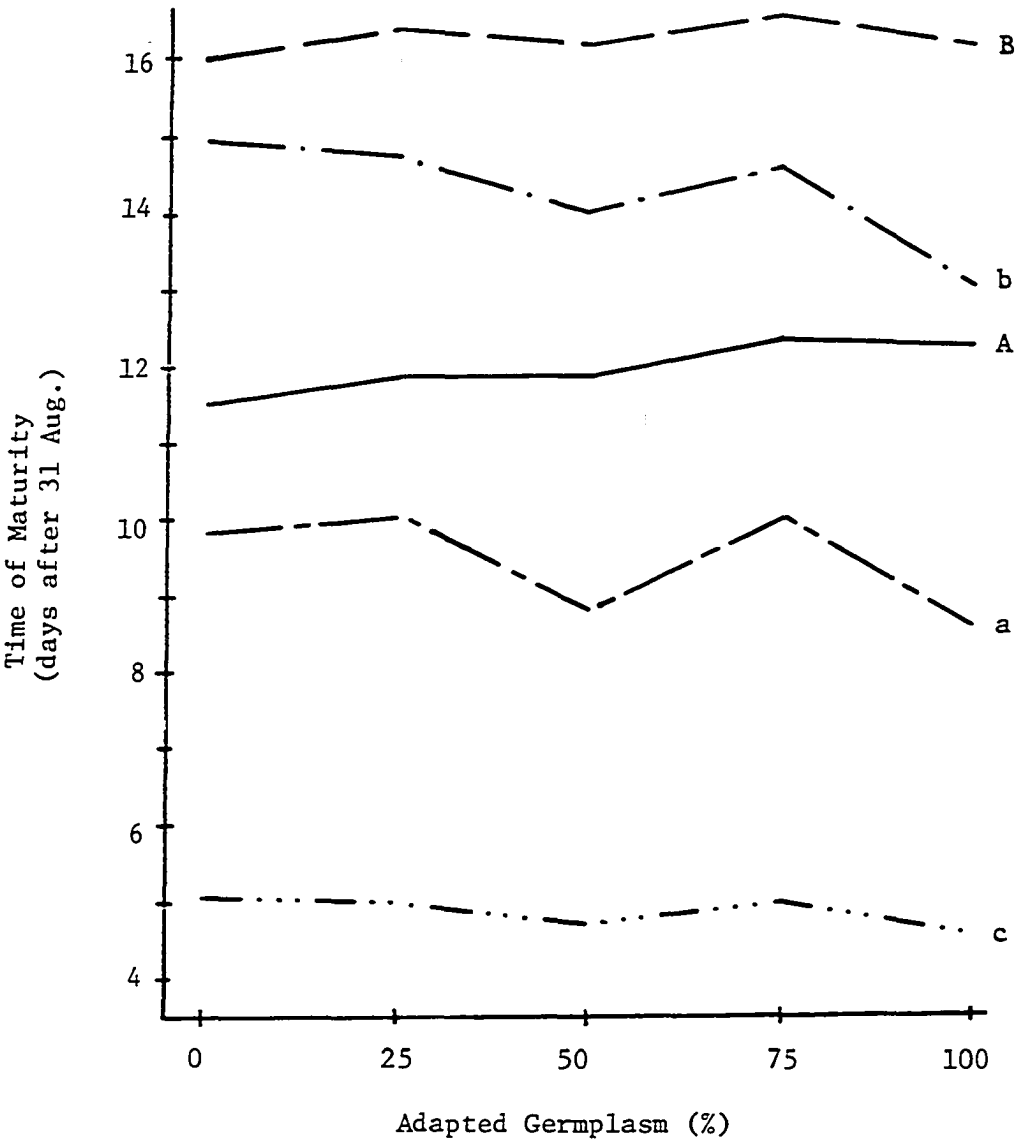


Figure 3. Mean time of maturity of the five populations using the complete entry set of 96 lines per population at (A) Ames, 1975, (B) Ames, 1976, and the partial entry set of 24 lines per population at (a) Ames, 1975, (b) Ames, 1976, and (c) Stuart, 1976

Table 13. Mean height and lodging score for Ames and Stuart, 1975, and Stuart, 1976, using the complete entry set of 96 lines per population and the partial entry set of 24 lines per population

	Complete entry set			Partial entry set			
	Ames 1975	Stuart 1975	Mean	Ames 1975	Stuart 1975	Stuart 1976	Mean
Height (cm)[1,2]							
AP1	87 d	64 e	76 c	85 b	62 c	74 a	74 ab
AP2	85 e	65 d	76 c	82 c	64 b	70 d	72 b
AP3	89 b	68 c	78 b	87 a	67 a	71 c	75 ab
AP4	88 c	69 b	79 b	85 b	65 b	72 b	74 ab
AP5	92 a	72 a	82 a	87 a	68 a	70 d	75 a
Mean	88	68	78	85	65	71	74
Lodging score[3]							
AP1	3.1 a	2.3 a	2.7 a	2.9 a	1.9 a	1.7 a	2.2 a
AP2	2.6 b	2.2 b	2.4 b	2.3 b	1.9 a	1.6 b	1.9 b
AP3	2.5 c	2.2 b	2.4 b	2.4 b	1.9 a	1.6 b	2.0 b
AP4	2.1 d	2.1 c	2.1 c	1.9 c	1.8 a	1.5 c	1.7 c
AP5	1.8 e	2.0 d	1.9 c	1.7 d	1.8 a	1.5 c	1.7 c
Mean	2.4	2.2	2.3	2.2	1.9	1.6	1.9

[1]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[2]Values followed by the same letter are not significantly different from each other at the 5% probability level according to Duncan's New Multiple Range Test.

[3]Scale of 1 (all plants erect) to 5 (most plants prostrate).

Table 14. Analysis of variance for height for the combined data for Ames and Stuart, 1975, using the complete entry set of 96 lines per population

Source of variation	Degrees of freedom		Mean squares	
Environment (E)	1		211932.1**	
Replication/E (R/E)	2		36.0	
Population (P)	4		3242.0**	
Linear		1		11485.1**
Quadratic		1		431.5
Lack of fit		2		525.8
E x P	4		119.6	
Error A	8		46.5	
Line/P[a] (L/P)	475		210.4**	
AP1		95		131.6**
AP2		95		209.2**
AP3		95		215.6**
AP4		95		272.3**
AP5		95		223.4**
E x L/P	475		67.2**	
AP1		95		71.1**
AP2		95		67.5**
AP3		95		69.9**
AP4		95		79.4**
AP5		95		48.3
Error B	950		44.0	
Corrected total	1919			

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

**F values are significant at 1% probability level.

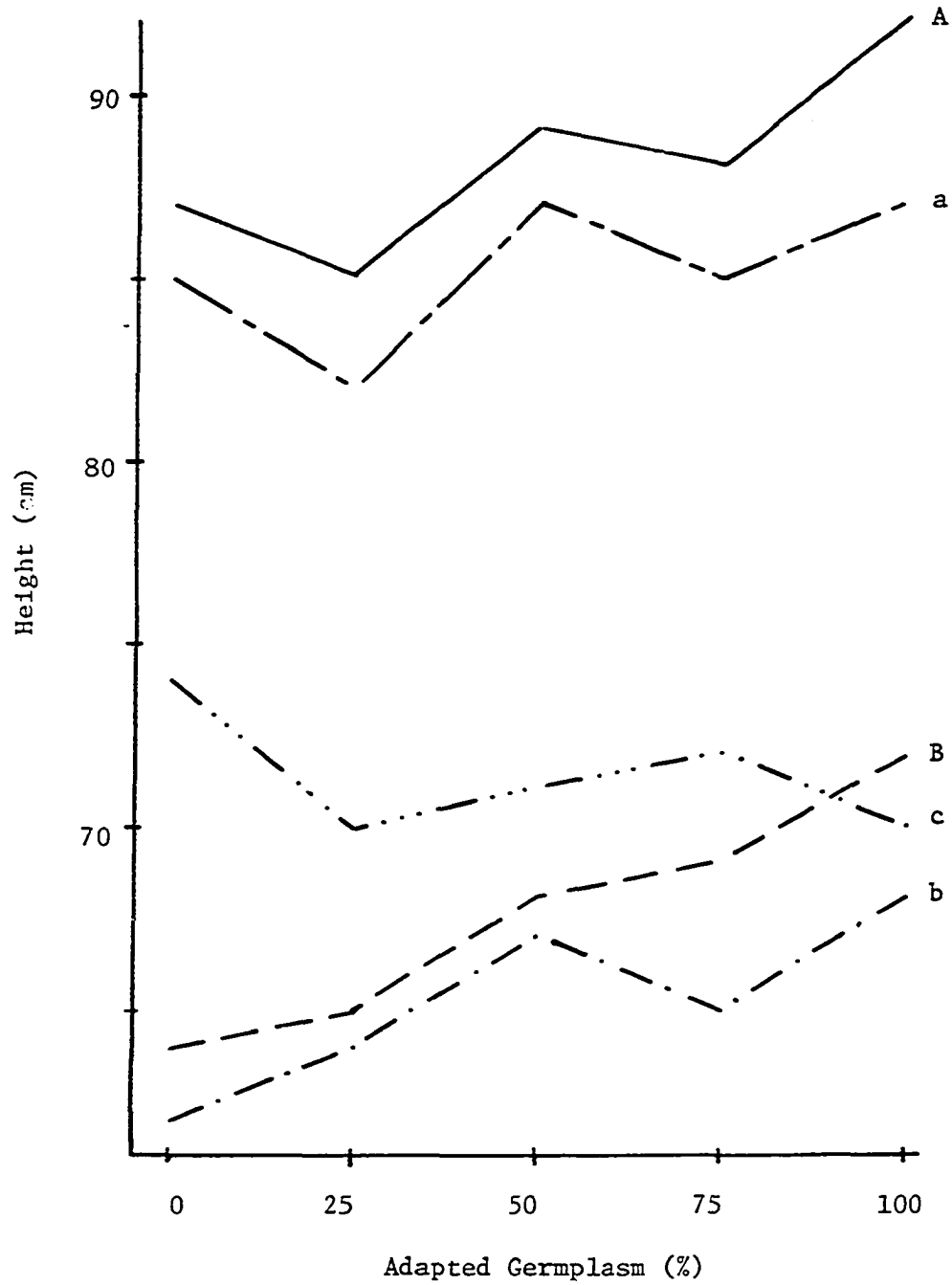


Figure 4. Mean height of the five populations using the complete entry set of 96 lines per population at (A) Ames, 1975, (B) Stuart, 1975, and the partial entry set of 24 lines per population at (a) Ames, 1975, (b) Stuart, 1975, and (c) Stuart, 1976

Table 15. Analysis of variance for height for the combined data for Ames and Stuart, 1975, and Ames, 1976, using the partial entry set of 24 lines per population

Source of variance	Degrees of freedom		Mean squares
Environments (E)	2		24844.7**
Replications/E (R/E)	3		621.4
Populations (P)	4		297.7
Linear		1	448.6
Quadratic		1	30.9
Lack of fit		2	355.7
E x P	8		194.1*
Error A	12		51.6
Lines/P[a] (L/P)	115		269.1**
AP1		23	164.2**
AP2		23	250.4**
AP3		23	335.3**
AP4		23	300.9**
AP5		23	294.7**
E x L/P	230		71.5**
AP1		46	82.8**
AP2		46	58.2**
AP3		46	89.9**
AP4		46	81.5
AP5		46	45.3
Error B	345		36.0
Corrected total	719		

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

*,**F values are significant at 5% and 1% probability levels, respectively.

Table 16. Estimated genetic variance and standard error for height and lodging for Ames and Stuart, 1975, using the complete entry set of 96 lines per population

	Ames 1975	Stuart 1975	Combined
Height (cm)[a,b]			
AP1	46.2 ± 9.8a	11.2 ± 6.3b	16.1 ± 5.3b
AP2	48.0 ± 10.2a	45.3 ± 10.7a	35.5 ± 7.9ab
AP3	51.1 ± 10.5a	47.6 ± 11.0a	37.1 ± 8.1ab
AP4	76.1 ± 13.9a	55.8 ± 12.1a	51.3 ± 10.1a
AP5	56.8 ± 11.2a	35.1 ± 9.3ab	39.0 ± 8.4ab
Lodging score[b,c]			
AP1	.20 ± .05ab	.29 ± .07a	.14 ± .04ab
AP2	.35 ± .07a	.42 ± .09a	.29 ± .06a
AP3	.25 ± .06a	.26 ± .06a	.17 ± .04ab
AP4	.22 ± .05a	.23 ± .06a	.18 ± .04ab
AP5	.04 ± .03b	.16 ± .05a	.05 ± .03b

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[b]Values followed by the same letter are not significantly different from each other since their ranges, as indicated by two standard errors on either side, overlap.

[c]Scale of 1 (all plants erect) to 5 (most plants prostrate).

Table 17. Estimated genetic variance and standard error for height and lodging for Ames and Stuart, 1975, and Stuart, 1976, using the partial entry set of 24 lines per population

	Ames 1975	Stuart 1975	Stuart 1976	Combined
Height (cm)[a,b]				
AP1	48.0 ± 19.9a	25.1 ± 13.6a	5.9 ± 2.4a	15.4 ± 8.1a
AP2	54.5 ± 21.7a	49.4 ± 20.0a	4.0 ± 1.9a	29.8 ± 12.1a
AP3	79.1 ± 28.4a	86.0 ± 30.2a	6.0 ± 2.5a	44.0 ± 16.0a
AP4	57.6 ± 22.5a	96.4 ± 33.1a	3.7 ± 1.9a	38.2 ± 14.4a
AP5	56.1 ± 22.1a	34.5 ± 16.0a	7.5 ± 2.9a	37.2 ± 14.1a
Lodging score[b,c]				
AP1	.21 ± .10a	.18 ± .08a	.03 ± .01a	.05 ± .03a
AP2	.29 ± .12a	.19 ± .09a	.02 ± .01ab	.08 ± .03a
AP3	.16 ± .09a	.04 ± .05a	.02 ± .01ab	.02 ± .02a
AP4	.08 ± .06a	.16 ± .08a	.00[d] ± .00b	.04 ± .03a
AP5	-.01 ± .05a	.10 ± .06a	.00 ± .00b	.00 ± .02a

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

[b]Values followed by the same letter not significantly different from each other since their ranges, as indicated by two standard errors on either side, overlap.

[c]Scale of 1 (all plants erect) to 5 (all plants prostrate).

[d]Less than .01.

had eight parents. Of these, AP4 would have had the lowest percentage of genes for a semi-determinate growth habit and, therefore, probably the greatest potential for expression of the genetic variability.

Lodging

The mean lodging score for the adapted parents was less than that for the unadapted parents (Table 4). The lower the percentage of adapted germplasm in a population, the greater the lodging (Table 13).

The environment x population interaction was highly significant (Tables 18 and 19). The analysis of variance showed a linear relationship between percentage adapted germplasm and lodging score. Though the slope of regression differed among environments, the pronounced linear trend was consistent (Figure 5).

The genetic variability for lodging was greatest in AP2 and lowest in AP5, but the differences were statistically significant only at Ames, 1975, and in the combined analysis, using the complete data set. Selection against lodging in the adapted parents would have been expected to have the greatest variability because it would have had the least contribution from the adpated parents of the three populations with eight lines in their parentage.

Table 18. Analysis of variance for lodging score for the combined data for Ames and Stuart, 1975, using the complete entry set of 96 lines per population

Source of variation	Degrees of freedom		Mean squares	
Environment (E)	1		26.22	
Replication/E (R/E)	2		7.51	
Population (P)	4		34.24	
Linear		1		133.54**
Quadratic		1		.01
Lack of fit		2		1.70
E x P	4		13.96**	
Error A	8		.36	
Line/P[a] (L/P)	475		1.10**	
AP1		95		.99**
AP2		95		1.60**
AP3		95		1.12**
AP4		95		1.15**
AP5		95		.65**
E x L/P	475		.44**	
AP1		95		.57**
AP2		95		.52**
AP3		95		.49**
AP4		95		.32
AP5		95		.31
Error B	950		.29	
Corrected total	1919			

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

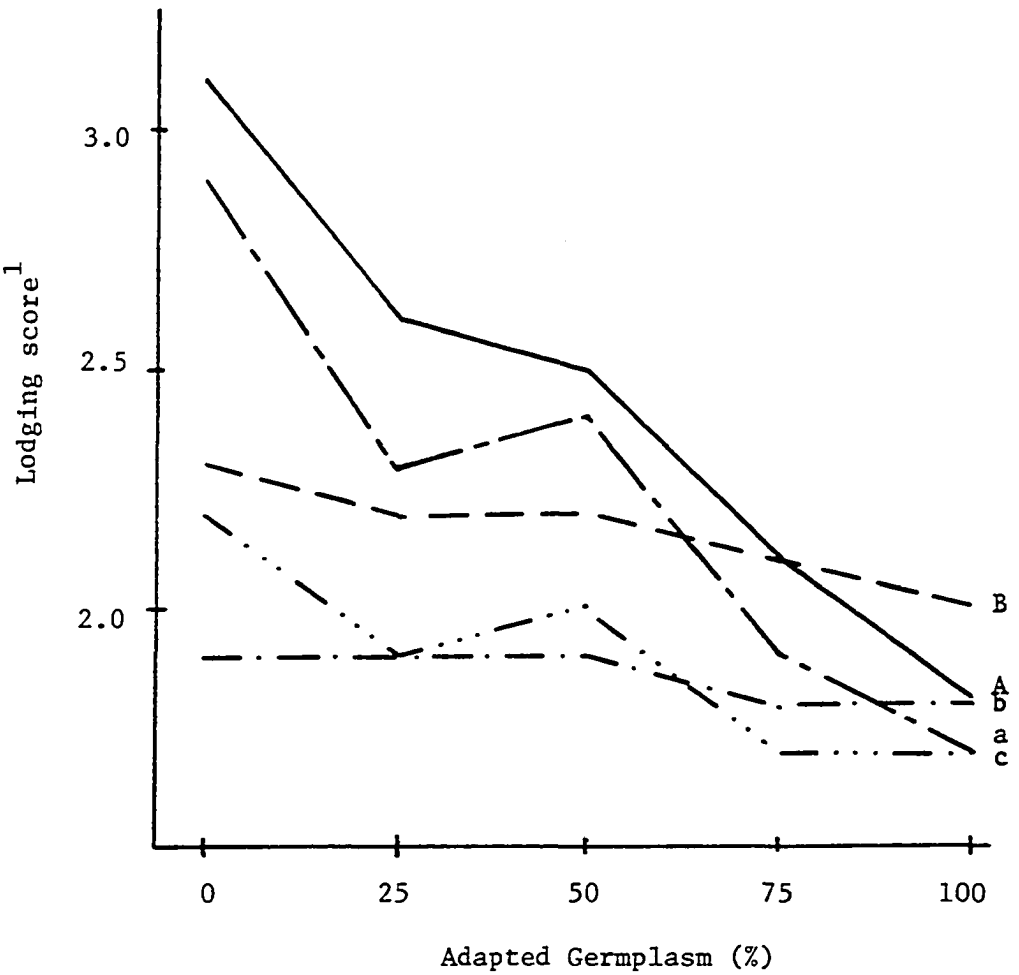
**F values are significant at 1% probability level.

Table 19. Analysis of variance of lodging score for the combined data set for Ames and Stuart, 1975, and Stuart, 1976, using the partial entry set of 24 lines per population

Source of variation	Degrees of freedom		Mean squares	
Environments (E)	2		24.75**	
Replications/E (R/E)	3		1.92	
Populations (P)	4		6.36	
Linear		1		23.20**
Quadratic		1		.02
Lack of fit		2		1.11
E x P	8		2.45**	
Error A	12		.20	
Lines/P[a] (L/P)	115		.50**	
AP1		23		.58**
AP2		23		.71**
AP3		23		.40
AP4		23		.53**
AP5		23		.28
E x L/P	230		.26**	
AP1		46		.35**
AP2		46		.37**
AP3		46		.24**
AP4		46		.20
AP5		46		.17
Error B	345		.15	
Corrected total	719			

[a]AP1 = 100%, AP2 = 75%, AP3 = 50%, AP4 = 25%, AP5 = 0% unadapted germplasm.

**F values are significant at 1% probability level.



[1]Scale of 1 (all plants erect) to 5 (most plants prostrate).

Figure 5. Mean lodging score of the five populations using the complete entry set of 96 lines per population at (A) Ames, 1975 (B) Stuart, 1975, and the partial entry set of 24 lines per population at (a) Ames, 1975, (b) Stuart, 1975, and (c) Stuart, 1976

DISCUSSION

The five populations were formed to study the effect of increasing percentages of unadapted germplasm in a breeding population. The adapted and unadapted parents were selected for their yield potential in Iowa (deMooy, 1962; Peterson, 1967). Unadapted lines are generally lower yielding than adapted cultivars. However, in this study the yields of the parents were not significantly different after correction for time of maturity.

The mean yields of the populations showed a decrease with an increasing percentage of unadapted germplasm. Although statistically significant, the maximum yield difference was only 197 kg/ha, using the complete data set, and 141 kg/ha from the partial data set (Table 6). In tabulating the four highest yielding lines from each set of 40 entries (top 10%) according to population of origin, 23 of the selected 48 lines for the complete entry set were from AP 5 (0% unadapted germplasm), 13 from AP4, 8 from AP3, 1 from AP2, and 3 from AP1. In the partial entry set, 5 of the 12 selected lines were from AP5, 2 from AP4, 3 from AP3, 1 from AP2, and 1 from AP1. The results were similar to those of MacKey (1963) who reported that crosses between unadapted and adapted lines generally produced more inferior segregates than crosses between adapted lines. Thorne and Fehr (1970b) reported a greater frequency of superior lines selected from soybean populations with 25% unadapted germplasm than from populations with 50% unadapted germplasm.

The highest yielding line in the test was a selection from AP2, the lowest yielding population. This indicates that although the frequency of occurrence may be low, superior lines may be available from a population with a large percentage of unadapted germplasm.

The greatest genetic variability for yield was in AP2 to AP4. The increased variability was probably due, in part, to the genetic diversity between the adapted and unadapted parents. More significant, however, may have been the fact that these three populations were formed with eight parents, whereas AP1 and AP5 had only 4 parents each. The individual contribution from both effects cannot be determined.

It was expected that AP1 (100% unadapted germplasm) would have the lowest mean yield. However, it was generally higher yielding than AP2 (75% unadapted germplasm) and sometimes greater than AP3 (50% unadapted germplasm). One explanation might be that the lines tested were not a random sample of the population. However, the mean height and lodging of AP1 fit the linear relationship with the other populations indicating that the sample was probably representative.

A second explanation considers each set of parents as representing a separate gene pool, an adapted germplasm pool and an unadapted

germplasm pool. The difference between the two would be based on source material and on the selection pressures imposed on each (Harlan et al., 1973). It would be expected that there would be more complementary gene action within each set than between them, especially among the adapted parents which had all been selected for high yield potential in similar environments. Less genetic complementation would be expected within the unadapted parent set since two of the varieties had the semi-determinate growth habit and the other two had the indeterminate growth habit.

Four to five generations of intermating would have effectively broken up many of the gene linkages and allowed for recombination (Hanson, 1959a,b). Matings between the two gene pools may have resulted in the formation of genotypes with less potential for high yield because the genetic relationship among the parents had been disrupted. In addition, due to the lesser complementation within the unadapted germplasm pool, progeny from AP1 would be less likely to be superior to the unadapted parents in yield than would the progeny from AP5 in relation to the adapted parent means. This depression in yield from the unadapted germplasm pool would be expected to slightly reduce yields in AP2 to AP4.

The practicality of incorporating unadapted germplasm into a breeding population depends on the goals of the project. The results of this study show that for short term breeding objectives, a 100% adapted population would produce more superior yielding lines, and the lines would be more agronomically acceptable.

Unadapted lines can be used in a long-term breeding program to broaden the genetic base. AP3 and AP4 yielded only slightly less than AP5 indicating that up to 50% unadapted germplasm could be incorporated into a population. The greater genetic variation for yield in AP3 and AP4 should permit more genetic gain through selection.

SUMMARY

Yield, height and lodging scores of five soybean populations were evaluated to determine the effect of the incorporation of increasing percentage of unadapted germplasm into a breeding population. The populations had different levels of unadapted germplasm, and ninety-six lines from each were grown in three environments.

The population means showed a small, but statistically significant decrease in yield with increasing percentages of unadapted germplasm. The population by environment interaction for yield was highly significant. Although most of the superior lines were identified from the populations with 0% and 25% unadapted germplasm, the highest yielding line was from the population with 75% unadapted germplasm. This would indicate that superior progeny can be selected from a population with a large percentage of unadapted germplasm, but the frequency of such lines is low. Genetic variance for yield was greatest in the populations that had both adapted and unadapted germplasm.

Height increased with increasing adapted germplasm reflecting the greater mean height of the adapted parents. Lodging scores increased with increasing percentage of unadapted germplasm.

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